

A global assessment of endemism and species richness across island and mainland regions

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Endemism and species richness are highly relevant to the global prioritization of conservation efforts in which oceanic islands have remained relatively neglected. When compared to mainland areas, oceanic islands in general are known for their high percentage of endemic species but only moderate levels of species richness, prompting the question of their relative conservation value. Here we quantify geographic patterns of endemism-scaled richness (“endemism richness”) of vascular plants across 90 terrestrial biogeographic regions, including islands, worldwide and evaluate their congruence with terrestrial vertebrates. Endemism richness of plants and vertebrates is strongly related, and values on islands exceed those of mainland regions by a factor of 9.5 and 8.1 for plants and vertebrates, respectively. Comparisons of different measures of past and future human impact and land cover change further reveal marked differences between mainland and island regions. While island and mainland regions suffered equally from past habitat loss, we find the human impact index, a measure of current threat, to be significantly higher on islands. Projected land-cover changes for the year 2100 indicate that land-use-driven changes on islands might strongly increase in the future. Given their conservation risks, smaller land areas, and high levels of endemism richness, islands may offer particularly high returns for species conservation efforts and therefore warrant a high priority in global biodiversity conservation in this century.

biodiversity | conservation | human impact | terrestrial vertebrates | vascular plants

Worldwide loss of biodiversity requires global conservation priority setting to channel limited international conservation resources to regions of highest conservation value and need for action (1–5). Approaches for using biological data as a component of priority setting vary but can largely be divided into (i) algorithm-based assessments such as minimum-area sets or gap analyses (2, 6–8) and (ii) index-based assessments using indices such as endemism or species richness as surrogates for the conservation value of a region (1, 4, 9). While many theoretical arguments underpin the strengths of algorithm-based assessments (2, 8, 10, 11), they require detailed distribution data that are only available for few taxonomic groups—almost exclusively terrestrial vertebrates (6, 9, 12–15), on which systematic conservation planning has thus relied increasingly in the past years. Such detailed data are not available for the vast majority of taxonomic groups on the global scale including vascular plants. Although great effort is being made in digitizing existing data from natural history collections for conservation purposes (16, 17), biodiversity loss is arguably proceeding more rapidly than the documentation of species distributions. Hence, an inventory-based approach, which forms a main basis for the present study, is a workable solution if global conservation planning is to be informed by vascular plants (18), a group of organisms which is of outstanding ecological and economical importance for human well-being (19).

Islands are well-known centers of range-restricted species and thus see high levels of endemism (20). However, they are simultaneously acknowledged for their lower species richness compared to

mainland areas (20). Hence, an index combining both endemism and species richness (“endemism richness”) can provide insight into the question of relative conservation value of islands and mainlands. Such an index has been calculated in a number of regional-to-continental-scale studies (21–25), which, however, have not focused on the differences between mainlands and islands. The basic concept of calculating endemism richness is to give each species the same value that is equally distributed across its range (21). For instance, when 100% of a species’ range, i.e., 1 range equivalent, falls into a mapping unit (such as a grid cell or, as in the present study, a biogeographic region), its entire value is attributed to this area. When half of the species’ distribution area falls into a mapping unit, only 50% of its value, or 0.5 range equivalents, are attributed to the mapping unit and so on. Summing up the fractions of range equivalents for all species within each mapping unit would then reflect both endemism and species richness (21, 26). In contrast to species richness, values of endemism richness on average show a linear relation with area at a given sampling scale and can thus be corrected for area disparity by linear conversion (21). Furthermore, unlike species richness or species endemism, the combined metric of endemism richness shows another useful property: The sum of all range equivalents of all mapping units yields the total number of species in the analysis—in our case, the global number of species in the studied taxa. Consequently, endemism richness can be interpreted as the specific contribution of an area to global biodiversity (21).

Here we calculated endemism richness of vascular plants for 90 biogeographic regions covering the entire terrestrial realm (except for Antarctica where the value is negligible). We compared our plant-based results to the spatial pattern of endemism richness of terrestrial vertebrates (amphibians, reptiles, birds, mammals) to quantify, for the first time, how well vascular plants capture the diversity of this charismatic group (and vice versa) and how taxon-specific differences might affect prioritization rankings. In this study, we specifically focused on comparing biodiversity of mainlands and islands because of the as yet undecided question of their relative conservation importance. Furthermore, islands are centers of past and imminent species extinction (27, 28), stressing even more the need for information on both biodiversity and specific threats in this part of the world.

Results and Discussion

Summing up the range equivalents of vascular plants for all 90 regions yields a total of 315,903. Given that the sum of range

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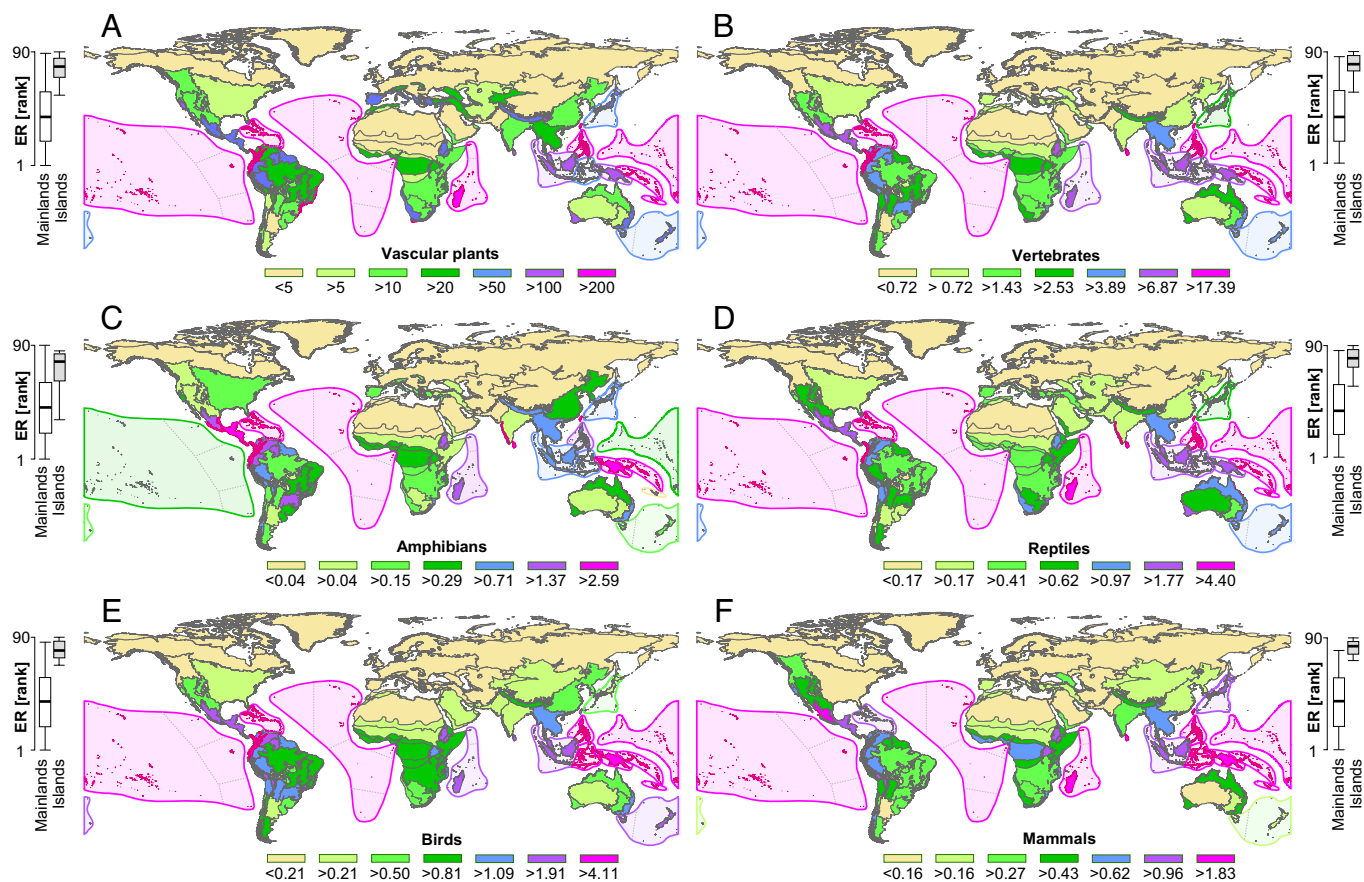


Fig. 1. Global patterns of endemism richness (ER; range equivalents per 10,000 km²) for (A) vascular plants, (B) terrestrial vertebrates, (C) amphibians, (D) reptiles, (E) birds, and (F) mammals across 90 biogeographic regions. Map legends were classified using quantiles, i.e., each color class contains a comparable number of regions. Box-and-whisker plots illustrate rank-based differences in endemism richness between mainland ($n = 76$; white boxes) and island regions ($n = 14$; gray boxes). Boxes mark second and third quartiles; whiskers mark the range of the data.

equivalents in the entire study area should be equal to the total number of species and assuming the data underlying our study accurately capture regional species numbers and degree of endemism, this suggests that recent estimates of global vascular plant richness ranging up to 422,000 species (29–31) may be too high. We found endemism richness of vascular plants to be geographically highly unevenly distributed (Fig. 1A) and it varied by 3 orders of magnitude (see Table S1). From a global perspective, the island of New Caledonia had by far the highest value with 1,350 range equivalents per 10,000 km²—a similar result has emerged from a coarse-scaled, grid-based study at the family level (32). Values were also high for other island regions, such as Polynesia–Micronesia, the Eastern Pacific, and the Atlantic Islands. Although accounting for only 3.6% of the terrestrial surface of the world, 26.1% of all range equivalents of plants are allotted to the 14 island regions. When standardized at 10,000 km², we found endemism richness to be 9.5 times higher on islands than in mainland regions (172.3 and 18.2 range equivalents per 10,000 km², respectively).

The island regions spanned a smaller latitudinal extent and were closer to the equator, possibly distorting the overall picture as species richness increases and average range size decreases toward the equator. We therefore repeated the calculation, restricting the mainland regions to the same latitudinal extent by excluding the 5 northernmost regions. As to be expected, this led to an increase in endemism richness on mainlands, but mainland regions still showed much lower average endemism richness (23.8 range equivalents per 10,000 km²).

Half of the top 20 regions in terms of endemism richness per standard area were island regions (Fig. 1A, Fig. S1). In fact, all but one (Japan) ranked among the top third of the 90 regions and all island regions had above average ranks ($F_{1,88} = 31.5, P < 0.001$; Fig. 1A). The top 30 regions contained 51.6% of the total range equivalents of vascular plants on only 7.4% of the Earth's terrestrial surface (Fig. 3A). Qualitatively similar spatial patterns of endemism richness across the 90 regions were also found for terrestrial vertebrates (Fig. 1B–F). Island regions had significantly higher endemism richness of vertebrates (8.1 times higher than for mainland regions) and islands contained 23.2% of the range equivalents of this group (Table S2). To test whether the plant-based delineation of biogeographic regions or the relatively coarse resolution of our mapping scheme had an effect on these findings, we divided up the 867 ecoregions (33) into mainlands and islands and compared their endemism richness. Endemism richness of island ecoregions for all 4 individual vertebrate classes and terrestrial vertebrates combined was significantly higher than for mainland regions (Fig. S2), which demonstrated that these results were robust toward the geographic delineation and across spatial scales.

Endemism richness of plants showed a relatively strong correlation with the entire group of vertebrates ($r_s = 0.83$), indicating a generally strong congruence of global patterns of endemism richness. The overall trend was similar, but stronger than recently found for patterns of richness (34). However, the degree of correlation within the 4 classes differed markedly (individual vertebrate classes: $r_s = 0.73$ – 0.82 ; Fig. 2 and Fig. S3). Furthermore, there were also striking exceptions, especially in the case of amphibians. The 4

A lot of data collecting and processing still needs to be accomplished to improve the accuracy of our knowledge on endemism richness on the global scale, especially for vascular plants. Only for 43 regions (48%), data quality was rated good or very good while being poor or very poor for 47 regions (Table S1). Overall, the data quality for the purpose of this study was better for island than for mainland regions: Ten of the 14 island regions (71%) had good or very good data quality. Partly, this might be attributed to the fact that islands are discrete spatial entities clearly defining the geographic extent of a study. In combination with their comparatively low species numbers, this may make islands more attractive to detailed floristic and faunistic inventorying and taxonomic work than less clearly defined, large mainland regions. It remains a great challenge that in most parts of the world, distribution data are only available for parts of the flora (45). Even the data set on Australian plant distributions, which is one of the best available continental data sets, covering about half of all known Australian plant species, has a pronounced geographic bias because of the absence of data from the Western Australian Herbarium (22). However, our approach of combining such “taxon-based” data sets with inventory data enabled us to partially address this problem by giving higher weight to inventory data whenever biases were known to exist in the taxon-based data and vice versa. Another potential source of error in the data might arise from the tendency to describe taxa as separate species on islands, artificially inflating endemism richness on islands in comparison to the mainland. However, quantitative studies testing this hypothesis are lacking and doubts remain as to whether this effect is important enough to explain the large differences in endemism richness between islands and mainlands.

Whenever priority setting and environmental impact assessments use endemism richness as a basis (e.g., when data are lacking or not of adequate quality for algorithm-based calculations), they should not rely on this criterion alone. Maximal representation and conservation of the global species pool will additionally benefit from taking into account further criteria such as biogeographic characteristics (2). Our study gives equal existence value to each species. However, for many purposes species’ importance may vary and be affected by attributes such as their phylogenetic and functional uniqueness (61, 62). Further, (nonglobal) local extinctions, which our study does not quantify, may have serious repercussions for ecosystem functions and services (63, 64). Attention should also be paid to the influence of spatial scale: We here identified regions with high values of endemism richness at a rather broad spatial resolution, but it remains a future challenge to optimize conservation strategies by systematic assessments of conservation priorities within these regions (17). Finally, in an era characterized by climate change and the loss of important biological and socioeconomic functions of ecosystems (65, 66), halting or even reversing these developments should be an equally important target of a global conservation strategy.

Materials and Methods

Delineation of Regions. Global patterns of endemism richness of vascular plants (i.e., ferns, gymnosperms, and angiosperms) and of terrestrial tetrapod vertebrates (amphibians, reptiles, birds, and mammals) were quantified across 90 biogeographic regions (14 island and 76 mainland regions). We divided the terrestrial realm into 90 regions on the basis of 4 criteria. First, we separated oceanic island areas from continental areas, but assigned islands with mainly continental floras to continents (e.g., Mediterranean islands, British Isles). The only case of a continental area assigned to an island region is Peninsular Malaysia, which was treated as a part of the Sundaland archipelago because this was deemed appropriate according to most of our delineation criteria. The other 3 criteria were biogeography, availability of data and, wherever appropriate, compatibility with boundaries of ecoregions (33) and biodiversity hotspots (5) for the data presented here to be usable within these frameworks and to enable direct comparisons with them. For a listing of the main biogeographical classifications used for the delineation of regions see Table S4. Islands were usually combined, mainly on the basis of the system of Conservation International (5). Furthermore, our aim was to avoid a delineation that results in island regions

which, although biogeographically distinct, are negligible in their level of total endemism richness from a global perspective. To this end, we formed island groups with at least 500 endemic species each by combining islands and archipelagos in the Atlantic Ocean, Polynesia, Micronesia, and the Eastern Pacific Ocean. To visualize biogeographical divisions within these island regions, they were displayed on the map as dotted lines (Fig. 1). Geographic data are available from authors on request.

Calculating Endemism Richness and Spatial Congruence of Cross-Taxon Patterns.

Endemism and species richness are widely used indicators of conservation value (1, 4, 53) and an index combining both has been calculated and mapped at regional-to-continental scales (21–24, 26) but not at the global scale. Because of its property of combining endemism and species richness, it is here called an index of endemism richness (21), whereas it has also been termed “range size rarity” (26) or “weighted endemism” (22, 23) in the literature. The standard method of calculating endemism richness (“taxon-based method”) is based on distribution data for single taxa within grid cells: For each grid cell, the inverse range sizes of all species occurring in that grid cell are summed up (24). Because of a lack of adequate distribution data, this method cannot be applied to vascular plant species at the global scale across all continents and island areas. An alternative calculation method (“inventory-based method”) is based on the number of species and endemics and on the chorology, i.e., the affiliation of a species to a broader biogeographic group such as “Holarctic element,” “Mediterranean endemic,” or “endemic to the Amazon basin” (21, 25). In our assessment of plant endemism richness, we combined both approaches, for 2 reasons. First, for the majority of regions data were only available to apply 1 of the 2 methods. Second, data for both approaches can include a certain level of error (e.g., because of weakly representative samples in range map databases), so counterchecking both types of data helped to improve the reliability of our results.

(i) Taxon-based method (plants and vertebrates): For several regions, large data sets with range maps of a large number of vascular plant species were available. Endemism richness was calculated as the sum of inverse range sizes (24) and then extrapolated to the total flora (e.g., by multiplying the resulting values by 20 when range maps were available for 5% of the flora) and corrected for area, using a standard area of 10,000 km² (21). Range size was measured as the number of grid cells or ecoregions in which a species occurs. Grid-based data sets were available for the following regions: Africa (67), Neotropics (68), Bolivia (69); a map with endemism richness values was available for Australia (22). Ecoregion-based data were available for Indo-Malayan (60). Distribution data for 26,586 terrestrial vertebrate species (4,792 amphibians, 7,506 reptiles, 9,585 birds, and 4,703 mammals) were derived from Wildfinder (70) for all 867 terrestrial ecoregions (33). Range size was measured as the total area of the ecoregions where a species was recorded. To investigate whether the plant-based delineation of the 90 regions or the rather coarse spatial resolution dictated by the limited data availability for plants had an effect on our analyses, we compared ecoregion-based values of vertebrate endemism richness separately (Fig. S2).

(ii) Inventory-based method (plants only): The flora of each region was divided into chorological groups based on the most detailed literature data available. The amount of range equivalents attributed to the region was calculated for each group as the fraction of the region compared to the assumed total distribution area of each chorological group multiplied by the number of species of the chorological group. The resulting values for all chorological groups were summed up to yield the total number of range equivalents for the region. This total figure was divided by the area size of the region in km² and multiplied by 10,000 to yield the number of range equivalents per 10,000 km². See ref. 21 for details.

Spatial congruence of cross-taxon patterns of endemism richness was assessed by pairwise comparisons of vascular plants and the 4 vertebrate classes using Spearman’s rank correlation coefficient (Fig. 2, Fig. S3). Additionally, we investigated the representativeness of plant-based rankings in capturing diversity patterns of vertebrates (Fig. 3).

Assessing Past and Future Threat for Mainland and Island Regions. We assessed past and future threats of island and mainland regions using different indices of land cover loss, human presence, and protection status from digitally available data sets. We used the Human Impact Index (HII) (51, 71), a composite measure of 8 global data layers referring to urban extent, population density, roads, navigable rivers, and agricultural land (spatial resolution: 1 km²). HII varies between 0 and 64 and refers largely to the year 2000. We also looked at the Human Footprint (51), which is the standardized version of HII by biome membership and obtained qualitatively and quantitatively similar results. Past habitat loss was assessed using a reclassified version of the Global Land Cover 2000 data set (72, 73) as the percentage of total land area classified as cultivated or managed, mosaics including cropland, and urban areas. As a proxy for protection status, we used the percentage of land area falling in the International Union for Conservation of Nature (IUCN) protected area categories I–VI (74). Future habitat loss was evalu-

ated for the year 2100 using the projections of the Millennium Ecosystem Assessment (52), which were averaged across all 4 socioeconomic scenarios. This data set allowed a comparison of climate change-driven and land use-driven (53, 75) changes in land cover. Changes in land cover were classified as climate change-driven or land use-driven (53, 75) and proportional changes were calculated across the 90 regions. All data sets were processed in a geographic information system (76). Data analysis was conducted using standard spreadsheet software and the software package R (77).

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